THE PREDATORY FEEDING BEHAVIOR OF THE CARINATED DOVE SNAIL *A. CARINATA* ON A VARIETY OF BENTHIC GASTROPOD EGG CAPSULES

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Abstract: A variety of studies have reported that many different predators prey on benthic egg capsules in the intertidal zone along the coast of the Eastern Pacific. The carinated dove snail *Alia carinata* has also been recently found to be able to consume the egg capsule embryos of *Lacuna marmorata*, however whether this behavior was a fluke or a common practice by the dove snail has yet to be studied. To study this behavior in more depth, multiple phases of an experiment were designed. First, we presented individual dove snails with one of seven food items: raw scallop, and the egg capsules of *Lacuna marmorata (early stage), Lacuna marmorata (late stage), Haminoea vesicula, Aeolidia loui, Nucella ostrina,* and *the egg capsules of the dove snail itself, Alia carinata*. Our predictions for this study were based on optimal foraging theory, a theory that tries to explain predator behavior by a model that prioritizes a predator's drive to have a net positive intake of energy over time. At the conclusion of our study, we were able to definitively show that the dove snail is able to consume the egg capsules of *N. ostrina, L. marmorata*, and *A. carinata*. The dove snail seemed to have a convincing preference for *L. marmorata* egg capsules across the board, and was also able to consume the egg capsules of *N. ostrina*, but only when it was the only food item available. This result indicates that *L. marmorata* egg capsules are a higher value food item than the egg capsules of *N. ostrina* under optimal foraging theory. Getting a better understand of the carinated dove snail's predatory egg capsule-eating habits will help conservationists in the future better protect intertidal gastropods and the habitats they live in.

Introduction

In the intertidal zones of the Eastern Pacific, many gastropod species lay benthic egg capsules on various types of vegetation or rock as an important part of their life cycle, but there have not been enough studies done on the mortality of these particular egg capsules after their progenitors leave. Unlike species that have internal gestation or parental care, benthic egg capsules are left to both the abiotic and biotic forces of nature. Egg capsules vary greatly in their morphology from species to species, especially in the size and shape of their external membranes. Egg capsule membranes have been linked to the reproductive energy of an animal, as producing a thicker and firmer membrane forces less energy to be available for embryo production (Rawlings 1990). Additionally, egg capsules protect the embryos inside from a variety of dangers, such as predation, disease, desiccation, and variation in salinity (Rawlings 1994).

Despite the supposed strength of egg capsule membranes, studies seem to indicate that these egg capsules are often subject to predation, as egg capsule predation rates of 50-70% have been reported, suggesting that egg capsules could be a high value food item for many species (Pechenik 1999). Some species that have identified as predators on egg capsules have been shore crabs, isopods, and hermit crabs (Rawlings 1990, Harmon & Allen 2018). In June 2022, the carinated dove snail *Alia carinata* was also recorded preying on the egg capsules of the periwinkle snail *Lacuna marmorata* by Jackie Sones and Dr. Eric Sanford for the very first time, proving that the dove snail is at least capable of preying on one type of benthic egg capsule.

The dove snail has been previously found to be a micro-carnivore and detritivores in coastal communities along the eastern Pacific from Alaska to Baja California (Haderlie et al. 1980), however very little else is known about the species. We wanted to expand on the

preliminary finding that the dove snail can prey on benthic egg capsules to discover whether the dove snail's observed behavior was a one time event or perhaps a common behavior along the California coast. To test this theory and to unearth more information about the dove snail's predatory feeding behavior, we created three hypotheses.

The first hypothesis we tested was that the dove snail would have the ability to feed on all of the food items that we presented to it, which we tested in phase 1 of our study. Our reasoning was that if the dove snail clearly had the adaptations necessary to feed on at least one gastropod's benthic egg capsule, then it makes sense that the same adaptations could be used on the egg capsules of other intertidal gastropods. We also considered the fact that the dove snail is relatively abundant in the areas that it is found on the California coast, so it would be difficult to support a large population of dove snails while only feeding on one particular food item, implying to us that the carinated dove snail was a generalist predator.

The second hypothesis we tested was that the dove snail would prefer egg capsules with a thinner membrane in phase 2 of our laboratory experiment. This hypothesis was based on the principles of the optimal foraging theory, where it is predicted that a predator will change their feeding behavior to maximize energy intake while minimizing the time spent searching and handling prey items (Pyke 2010). For this hypothesis, we focused specifically on the dove snail's handling time while consuming egg capsules. Our prediction was that egg capsules with thinner membranes would be easier for the dove snail to drill into and would result in the dove snail spending less time consuming the embryos inside the egg capsules.

Finally, the third hypothesis we examined was that the dove snail would prefer raw scallop when given the option of consuming scallop pieces or the various egg capsules provided. We had this prediction because many similar intertidal animals are opportunistic scavengers, and

we believed that the dove snail would have to spend less energy consuming the scallop than drilling through the membranes of the egg capsules. Spending less time and energy searching and handling food results in a higher energy intake for the dove snail according to the optimal foraging theory (Pyke 2010).

Materials and Methods

Animal and Egg Capsule Collection

Prior to the beginning of our lab experiment, we collected 28 *Alia carinata* individuals from the low intertidal pools present along Horseshoe Cove in Bodega Bay, CA. We then measured the shell length of each dove snail lengthwise using a caliper and matched each measurement with a random dove snail identification number (DS 1-28). In a tide pool directly adjacent to where we found the dove snails, we collected 20 *A. carinata* egg capsules. We also collected approximately 71 *Lacuna marmorata* egg capsules laid on surf grass at the same location and counted 40 early stage and 31 late stage egg capsules. We were able to identify what stage of its life cycle the embryos were in by the distinctive colors of *L. marmorata* egg capsules. While the early stage egg capsules are a bright minty green, the later stage egg capsules are a milky white or grey color. To remove the *L. marmorata* egg capsules from the surf grass beds, we used our fingernails to break off pieces of the surf grass near the egg capsules to minimally disturb the samples. Between the time we ended phase 1 and began phase 2, many of the early stage *L. marmorata* egg capsules had developed into the late stage. We then traveled to Tomales Bay, where we collected 32 *Haminoea vesicula* egg capsules that were laid on eel grass in the mudflats found there. Again, we were able to very easily tear off the pieces of eel grass that had egg capsules attached by using our bare hands. Next, we found our *Nucella ostrina* egg capsules

around mussel beds in a wave exposed region on the Bodega Marine Reserve. We looked in areas known to have a high density of *N. ostrina* individuals, and collected 90 *N. ostrina* egg capsules by scraping them off of rocks with a micro-spatula. Unfortunately, we were unable to find any *N. ostrina* egg capsules that were attached to any vegetation. We then collected 6 *Aeolidia loui* individuals from Pinnacle Gulch, also in Bodega Bay, CA, and brought them back to the lab to have them lay egg capsules. We collected individuals instead of the egg capsules directly, as many nudibranch species have egg capsules that are morphologically very similar and we wanted to be certain of the origin of the egg capsule we collected. Two *A. loui* individuals each were placed in three separate containers containing kelp to encourage the animals to lay egg capsules on vegetation. Finally, we bought our raw scallop from The Tides Market in Bodega Bay, CA, and cut them into small 5x5x5mm cubes. When not in active use, the scallops were kept in a refrigerator unit.

For all of the egg capsules we collected, we put one kind of egg capsule in separate plastic containers with mesh openings on the sides, and placed those containers randomly in a large tub with running seawater. We placed all containers in the same seawater tub to standardize the water temperature experienced by all samples, and to avoid general desiccation of our samples.

Phase 1: Dove Snail Feeding Ability

We did our study in two distinct phases in order to study both the feeding abilities of the dove snail as well as its preference for a variety of food items. After the initial 77 hour dove snail starvation period, we began the first trial of the first phase of our experiment. The purpose of the first phase of our study was to determine which food items the dove snail was physically able to consume when left with no other choices. The food items that the dove snail could consume were

then used for our choice experiment in phase 2. We did 4 replications of 6 different food item treatments in our first trial for a total sample size of 24. The food items we chose included raw scallop and the egg capsules of *Lacuna marmorata* (early and late stage), *Nucella ostrina, Alia carinata,* and *Haminoea vesicula*. Notably, we were unable to include the egg capsules of *A. loui* in the first trial of this phase, as the *A. loui* individuals we had previously collected had not yet begun laying egg capsules. After organizing all of the food items randomly into 24 individual lidded mesh containers, we added a blade of surf grass to each of the 4 containers holding *Nucella ostrina* egg capsules to control for the possible effect that vegetation may have on the dove snail's ability to feed. After sorting our food items into mesh containers with lids, we used a microscope camera to take initial photos of every egg capsule next to a small 10 millimeter ruler to have a sense of scale for area calculations later on. Specifically for the *N. ostrina* egg capsule final microscope images, we took photos of both sides of the egg capsule to get a clear image of all of the holes that the dove snail may have drilled.

Next, we randomly placed 24 dove snails into the 24 prepared lidded mesh containers. We left these 24 trial 1 containers in the seawater tank for 48 hours to allow the dove snails a sufficient amount of time to consume their respective food items. After this trial concluded, we again took photos of all of the food items with a microscope camera to measure final egg capsule area consumed by the dove snails in our analysis. We then returned the dove snails to individual containers in the sea water tank, and left them without food for 24 hours before the next trial.

For the second trial of the first phase of our study, we repeated the same methods except we did 4 replicates of 7 different food item treatments for a total sample size of 28. In addition to the 6 previously mentioned food items we used in trial 1, we also were able to use the egg capsules of the nudibranch *A. loui*, as the individuals we had kept in the lab had laid egg capsules

at this point. Unfortunately only 1 of the nudibranch egg capsules was laid directly on kelp, so in the other 3 treatments we added a blade of surf grass as a control.

Phase 2: Dove Snail Food Preference

After a 24 hour rest period, we began phase 2 of our experiment which was focused on studying the feeding preferences of the dove snail when given a choice between multiple different food items. We excluded any food items that were not eaten in phase 1 as they would only complicate our phase 2 findings, and were left with raw scallop and the egg capsules of *L. marmorata* (late development), *N. ostrina, and A. carinata.*

For the first trial of phase 2, we created 8 replicates of the same treatment. This treatment consisted of a small glass bowl containing the 4 previously mentioned food items as well as small rocks to weigh down the surf grass that had egg capsules. We then took initial photos of all of the replicates with a microscope camera in the same way as phase 1. Dove snails were then added to the 8 replicate bowls, and the bowls were placed in running seawater on a seawater table to keep temperature constant across every replicate. The bowls were left for 24 hours to allow the dove snails time to start consuming their preferred food choice. Again, microscope photos were taken of all food items next to a 10mm ruler for scale. After 24 hours, we transferred the 8 replicate bowl treatments into tea strainer containers as only 2/8 of the dove snails in this trial had begun consuming any of the food items. At the conclusion of this trial, final 48 hour images were taken of the food items.

In trial 2 of our food item preference study, we randomly put dove snails and the 4 chosen food items in small mesh containers with lids in a large tub with running seawater. These containers were fully submerged to maintain constant temperature and moisture levels. Microscope photos were again taken before the beginning of the trial, as well as at the 24 and 48

hour marks. To ascertain the chosen food item in each replicate of phase 2, we compared the initial microscope images of the food items with the images taken after 24 and 48 hours and looked specifically for missing embryos or other evidence of dove snail predation.

Data Collection and Analysis

At the conclusion of our study, we were left with initial and final microscope photos of every food item used in phase 1, as well as initial, 24 hour, and 48 hour microscope photos from phase 2. To turn our egg capsule photos from images into quantifiable data, we used ImageJ imaging software to trace the two dimensional area of every food item as an estimation of biomass, however we measured egg capsule area in a more particular way. We noticed in our preliminary study that dove snail consumption did not have a large influence on the actual membrane of the egg capsules, but rather on the embryo mass inside the egg capsule membrane. Based on this information, we measured the area of the egg capsules using the visible embryo mass inside of the egg capsule, rather than the exterior membrane. While this method does not take into consideration the three dimensional form that all of our food items had, it allowed us to easily compare images of the egg capsules at different times in our study to calculate a change in total area.

To calculate the percent of total embryos that the dove snails consumed between the initial and final images in phase 1, we used the equation "(initial embryo area – final embryo area)/initial embryo area". This equation standardized the egg capsules so that regardless of size, the percentage of embryos eaten was comparable across all of the different egg capsules. We then applied an arcsine square root transformation to this data to account for the low variance in embryo consumption and to refine the data set. However, despite this transformation our data did not align with the assumptions of an ANOVA test, but our ANOVA test still provided sufficient

analysis when comparing the statistical differences in embryo consumption between our phase 1 treatment groups. To calculate feeding rate in phase 2, we used the equation "(initial embryo area – 24 hour embryo area)/initial embryo area" to determine the percentage of embryo mass consumed in the first 24 hours of this phase. To calculate the feeding rate in the second 24 hours of our study, we used the equation "(24 hour embryo area – 48 hour embryo area)/initial embryo area".

We also wanted to qualitatively categorize the egg capsules by membrane form, so we used a micro-spatula in our preliminary observations to prod the egg capsule membranes until they broke. We also attempted to measure the membrane thickness of *L. marmorata* and *H. vesicula* by freezing 6 egg capsules of each species and using a scalpel to cut a cross section out of the egg capsules. Unfortunately, there was no clear separation between the edge of the membrane and the embryo mass so we were unable to directly measure the thickness of the egg capsule membrane.

Results

Phase 1

From our small pilot examination of the egg capsule membranes, we found that the egg capsules of *H. vesicula, L. marmorata, and A. loui* had a gelatinous, jelly-like consistency and the egg capsule membrane disintegrated quickly after penetration. In stark contrast, the egg capsules of *A. carinata* and *N. ostrina* had a rubbery, rigid membrane comparable to hard plastic, and did not change shape after penetration.

The dove snails were able to consume every food item except for the egg capsules of *Aeolidia loui* and *Haminoea vesicula.* Among the food items that the dove snails were able to

consume, they consumed the egg capsules of *Nucella ostrina* at the lowest frequency and the scallop pieces and egg capsules of *Lacuna marmorata* and *Alia carinata* at the highest frequency (75% vs. 100%; Fig.1). We had 8 replicates of every food item except for the egg capsules of *Aeolidia loui*, of which we only had 4 replicates due to our limited supply of individuals from that species.

Of the 4 different types of egg capsules that the dove snail was capable of consuming, it consumed significantly more of the early stage *Lacuna marmorata* embryos than *Nucella ostrina* embryos on average (Tukey HSD, p => 0.0001; Fig. 2). However, there was no significant difference in the mean amount of embryos the dove snail consumed between *Lacuna marmorata* early stage, *Lacuna marmorata* late stage and *Alia carinata* egg capsules, and no significant difference between *Lacuna marmorata* late stage egg capsules and the egg capsules of *Nucella ostrina* and *Alia carinata.*

Dove snail size had no significant difference across every food choice treatment and replicate in both phases of our study (ANOVA, $F_{6, 45} = 1.7442$, $p > 0.0001$; Fig. 3).

Phase 2

In our phase 2 choice experiment dove snails consumed 46.64% of the embryos in *Lacuna marmorata* egg capsules in the first 24 hours of the study on average, and only consumed an average of 8.72% more embryos in the second 24 hours (t-test, $t_{43.157} = -4.042$, $p < 0.0001$; Fig. 4).

When presented with a selection of food items, 71.43% of the 28 dove snails used in this experiment preferred the *Lacuna marmorata* late stage egg capsules first, while only 28.57% of the dove snails preferred the scallop first (Fig. 5). None of the dove snails in this phase preferred

the egg capsules of *Nucella ostrina* or *Alia carinata*, however two individual dove snails did consume a noticeable amount of *Alia carinata* egg capsules.

Discussion

Phase 1: Dove Snail Feeding Ability

The first hypothesis we tested was that the dove snail would have the ability to eat all 7 of the food items (Fig. 6) we presented to it. The food items we chose for this phase of our experiment were a piece of scallop and the egg capsules of *Lacuna marmorata* (early stage), *Lacuna marmorata* (late stage), *Nucella ostrina, Alia carinata, Aeolidia loui*, *Haminoea vesicula,* and raw scallop. This hypothesis turned out to be false, as in our phase 1 study we discovered that the dove snail was only able to eat 5 of the 7 chosen food items (Fig. 1). Prior to the start of our experiment, we were confident that the dove snail would be able to consume both the early and late state *L. marmorata* egg capsules, as Jackie Sones had captured this behavior on video in June 2022 at the Bodega Marine Laboratory, so this was not surprising. In fact, the dove snail ate an average of 99.52% and 92.05% of the early and late stage *L. marmorata* embryos respectively, implying a strong ability to eat that particular type of egg capsule (Fig. 2). There was no significant difference between the percentage of embryo mass consumed in the *L. marmorata* early stage treatments when compared to the *L. marmorata* late stage treatments, showing that the dove snail did not consume one *L. marmorata* embryo mass more than the other (Tukey HSD, $p = 0.0160$; Fig. 2). This result suggests that the *L. marmorata* egg capsule's developmental stage does not have a significant effect on the dove snail's feeding behavior.

The dove snail was observed to cannibalistically consume its own young at a frequency and percentage of embryos eaten similar to its predation on the egg capsules of L. marmorata

(Fig. 1 & 2). This was a striking result, as the membrane of *L. marmorata* egg capsules was qualitatively found to be much less rigid, and thus theoretically easier to drill through, than *A. carinata* egg capsules. We hypothesize that because the dove snail is in such close proximity to its own species' egg capsules in every environment it inhabits, it may have evolved specific adaptations that allow it to cannibalize its own species' young more efficiently. These adaptations may also be important as the dove snail cannibalizing the young of intraspecies competitors could increase an individual's fitness, however more studies would have to be done to prove this concept.

We were also confident in our prediction that the carinated dove snail would be able to eat the raw pieces of scallop that we provided, as many marine animals are opportunistic scavengers and detritivores. Unfortunately, due to the degradation and dove snail consumption of the scallop samples we used over this 48 hour period of the study it was impossible to accurately measure the difference in scallop area between the initial and final parts of the trial. In fact, several times we measured a final area larger than the initial area, which indicated an error in our method of 2 dimensional area measurement at least when applied to the pieces of scallop. We hypothesize that due to general deterioration and dove snail feeding, the scallop flesh was broken apart and expanded and thus did not accurately represent how much of the scallop was actually consumed. Despite this, we were able to determine that 100% of the scallop pieces in this phase were eaten to some degree from distinguishable bite marks and holes left in the leftover scallop flesh (Fig. 1).

The two food items that the dove snail was not able to consume at all across every replicate were the egg capsules of the nudibranch *Aeolidia loui* and the bubble snail *Haminoea vesicula* (Fig. 1). This result was surprising to us, as the egg capsules of both A. loui and H.

vesicula have qualitatively weaker membranes than the egg capsules of N. ostrina, which the dove snail was able to eat. We theorize that the egg capsules of the nudibranch *A. loui* may have been chemically defended as another nudibranch species, *Hexabranchus sanguineus*, uses chemical defenses obtained from sponge macrolides to protect their egg capsules (Pawlik et al. 1988). So, it is possible that *A. loui* uses a chemical compound from the anemones they prey on to defend their egg capsules as well. We also considered that the egg capsules of *H. vesicula* may have chemical defenses, however it is also likely that chemicals that are used to defend larvae from predators may also harm the larvae themselves (Pechenik 1999). Additionally, *A. loui* egg capsules collected from the field were covered in dirt and mud from the Tomales Bay mudflats, which may have had an influence on the egg capsule's palatability to the dove snail. At the conclusion of phase 1 we found that many of the *H. vesicula* egg capsules had a noticeable amount of mud particulates disappear compared to the initial images, despite the egg capsule's membrane never being pierced. This observation suggests that while the dove snail did show interest in the *H. vesicula* egg capsule, the egg capsule was still inedible to the dove snail. More research needs to be done to investigate the adaptive purpose that mud particles may have in protecting *H. vesicula* egg capsules from predation.

In the final images of many of the egg capsules consumed by the dove snail, a handful of embryos were found to remain. Specifically in both the early and late stage *L. marmorata* treatments, 0.48% and 7.95% of the embryos remained after feeding on average (Fig. 2). This statistic suggests that the dove snail may receive diminishing returns of energy with regard to the optimal foraging theory as the egg capsule becomes more and more empty. Theoretically, the dove snail would have to extend handling time to consume the last few embryos left in an egg capsule, which likely is not worth the energy cost as the dove snail continues to search for more

food elsewhere. This is also supported by the fact that the dove snail ate significantly less *L. marmorata* embryos in the second 24 hours of phase 2 when compared to the first 24 hours of phase 2 (8.72% vs. 46.64%; Fig. 4).

Phase 2: Dove Snail Food Preference

The second hypothesis that we tested in our study was that the dove snail would prefer egg capsules with a thinner membrane to minimize handling time in our phase 2 choice study. Our results suggest that this may be true, as the dove snail's preferred food choice was late stage *L. marmorata* egg capsules 71.43% of the time, and they never preferred the egg capsules of *N. ostrina* or *A. carinata* (Fig. 5). We chose to only use late stage *L. marmorata* egg capsules in phase 2 of our study, as there was no significant difference in the frequency of consumption or percentage of embryos consumed between the early and late stage *L.* marmorata egg capsules in phase 1 (Fig. 1 & 2). We previously determined that *L. marmorata* had a relatively weak membrane when compared to *N. ostrina* and *A. carinata*, but we were unable to accurately determine the thickness of each egg capsule membrane so we cannot conclusively state that the dove snail preferred egg capsules with thinner membranes.

While the dove snail clearly has the ability to consume the egg capsules of *N. ostrina* as indicated by our phase 1 study, not a single *N. ostrina* egg capsule was penetrated when the dove snail was given a selection of food items in our phase 2 study. This result strongly suggests that the dove snail will only consume *N. ostrina* egg capsules when given no other food options. We hypothesize that this extreme difference in *N. ostrina* embryo consumption in phase 1 and phase 2 is due to the difference in handling time and energy intake per embryo mass between *L. marmorata* egg capsules and *N. ostrina* egg capsules. According to the optimal foraging theory, a predator will attempt to minimize handling time and maximize energy intake per prey item

(Pyke 2010). We minimized the effect that search time may have on the energy intake of the dove snail by using small enclosures for all of our food treatments, which allowed us to focus on handling time and energy intake per prey item.

While we determined that *L. marmorata* egg capsules have a relatively weak membrane, they also have a high embryo mass relative to their egg capsule size. The weaker membrane could allow the dove snail to drill into the egg capsule more quickly using its radula, reducing handling time. The high embryo mass relative to egg capsule size means that there is a low volume of egg yolk relative to the high density of *L. marmorata* embryos, which may allow the dove snail to consume the embryos more quickly, further reducing handling time. As handling time decreases, the value of *L. marmorata* egg capsules as a food item increases. In contrast, *N. ostrina* egg capsules have a relatively strong membrane and a low embryo mass relative to egg capsule size. The tougher membrane could result in the dove snail taking a longer time to bore into the *N. ostrina* egg capsules, increasing handling time. The low embryo mass relative to egg capsule size of *N. ostrina* means that there is a large amount of empty space in their egg capsules, which could contribute to a longer handling time of the egg capsule as the dove snail uses its proboscis to search for the embryos within the egg capsule. In addition to handling time, the nutritional value of each species' embryos could also play a substantial role in which egg capsule the dove snail chooses to feed on according to the optimal foraging theory (Pyke 2010), however we were unable to collect the nutrition value of each type of embryo within the scope of our study.

The *A. carinata* egg capsules were consumed in only 2 of the 28 phase 2 replicates, indicating that the dove snail did not have a noticeable preference for this egg capsule when given other food item choices. However, we were unable to determine if *A. carinata* embryos

were truly consumed in this phase, or just hatched due to an extended time spent in the lab. This ambiguity over the fate of the absent embryos is due to the morphology of *A. carinata* egg capsules. Each egg capsule has a transparent bubble on the top of it (blue arrows; Fig. 7) that we initially believed was a radula drilling hole, until we compared images from different time points of the study. We now believe that the dove snail bores through the side of the *A. carinata* egg capsule, which we hypothesize to be due to a weaker membrane in those locations. However, due to our two dimensional strategy for taking images of the egg capsules it is often not possible to observe these drill holes (red arrows; Fig. 7) in the sides of the *A. carinata* egg capsules. This observation makes it unfeasible to assume that the embryos absent in the final photos of phase 2 were eaten by the dove snail rather than naturally hatching.

Dove snail size did not affect our results, as we found that average dove snail size across every food item treatment and phase did not have significant variation (Fig. 3). While we did originally predict that larger dove snails may be able to drill tougher membranes or consume larger egg capsules, due to our randomization at multiple stages of our experiments this was found to be false.

Finally, the third hypothesis that we tested was that when given the option between egg capsules and scallops, the dove snail would choose to consume the scallops. This hypothesis was proven to be false, as the dove snail preferred the late stage *L. marmorata* capsules significantly more than the raw scallop (71.43% vs. 28.57%; Fig. 5). This was an interesting result, as we had predicted that a piece of scallop would be much easier to consume than an egg capsule protected by a membrane. However according to optimal foraging theory, a predator will try to maximize its energy intake per prey item (Pyke 2010), suggesting that *L. marmorata* egg capsules are a higher value food item than the scallop, even when handling time of the food item is factored in.

Conclusion

Throughout our study, the carinated dove snail *Alia carinata* has shown itself to be an insatiable predator on a variety of benthic egg capsules, with a particularly strong affinity for the egg capsules of the periwinkle snail *Lacuna marmorata.* The dove snail has also been found to be able to drill through the tough membranes of *Nucella ostrina* egg capsules, as well as the membranes of its own species' young, *Alia carinata*. Our study represents the first step in better understanding the predatory egg capsule-eating behavior of the dove snail, so predictably there are still many questions left to answer. We still are unable to definitively determine the dove snail's preferred technique for finding (sight or chemosensory detection) or drilling into egg capsules, how long it takes the dove snail to consume its prey, and whether the dove snail can prey on an even greater variety of benthic egg capsules. Knowledge of the dove snail's abundance on the Eastern Pacific coast could greatly influence conservation efforts in the future, as the dove snail's exact impact on the populations dynamics of gastropods has yet to be studied. Future studies on the carinated dove snail are then required if we want to fully understand the life cycles of intertidal gastropods, as well as the biotic risks that benthic egg capsules face in the intertidal zone.

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Literature Cited

Haderlie, E. C., Morris, R. H., & Abbott, D. P. (1980). *Intertidal invertebrates of California*. Stanford Univ. Press.

Harmon, E., & Allen, J. (2018). Predator-induced plasticity in egg capsule deposition in the mud snail tritia obsoleta. *Marine Ecology Progress Series*, *586*, 113–125. https://doi.org/10.3354/meps12368

Pawlik, J. R., Kernan, M. R., Molinski, T. F., Harper, M. K., & Faulkner, D. J. (1988). Defensive chemicals of the Spanisch dancer Nudibranch Hexabranchus sanguineus and its egg ribbons: Macrolides derived from a sponge diet. *Journal of Experimental Marine Biology and Ecology*, *119*(2), 99–109. https://doi.org/10.1016/0022-0981(88)90225-0

Pechenik, J. (1999). On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, *177*, 269–297. https://doi.org/10.3354/meps177269

Pyke, G. H. (2010). Optimal foraging theory: Introduction. *Encyclopedia of Animal Behavior*, 601–603. https://doi.org/10.1016/b978-0-08-045337-8.00210-2

Rawlings, T. A. (1990). Associations between egg capsule morphology and predation among populations of the marine gastropod, *nucella emarginata*. *The Biological Bulletin*, *179*(3), 312–325. https://doi.org/10.2307/1542323

Rawlings, T. A. (1994). Encapsulation of eggs by marine gastropods: Effect of variation in capsule from on the vulnerability of embryos to predation. *Evolution*, *48*(4), 1301. https://doi.org/10.2307/2410387

Figures

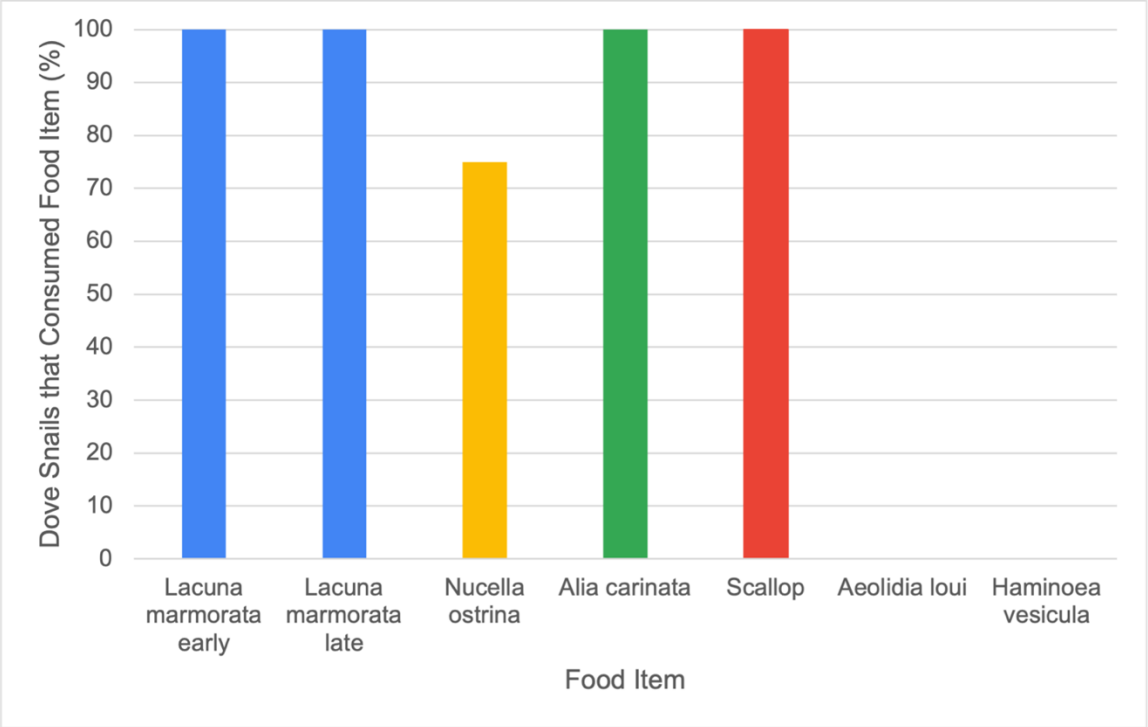

Figure 1: The percentage of dove snail individuals that were definitively able to consume the food item on the x-axis out of 8 replicates in phase 1, except for A. loui *which only had 4 replicates. Colors of the bar graphs correspond to food item.*

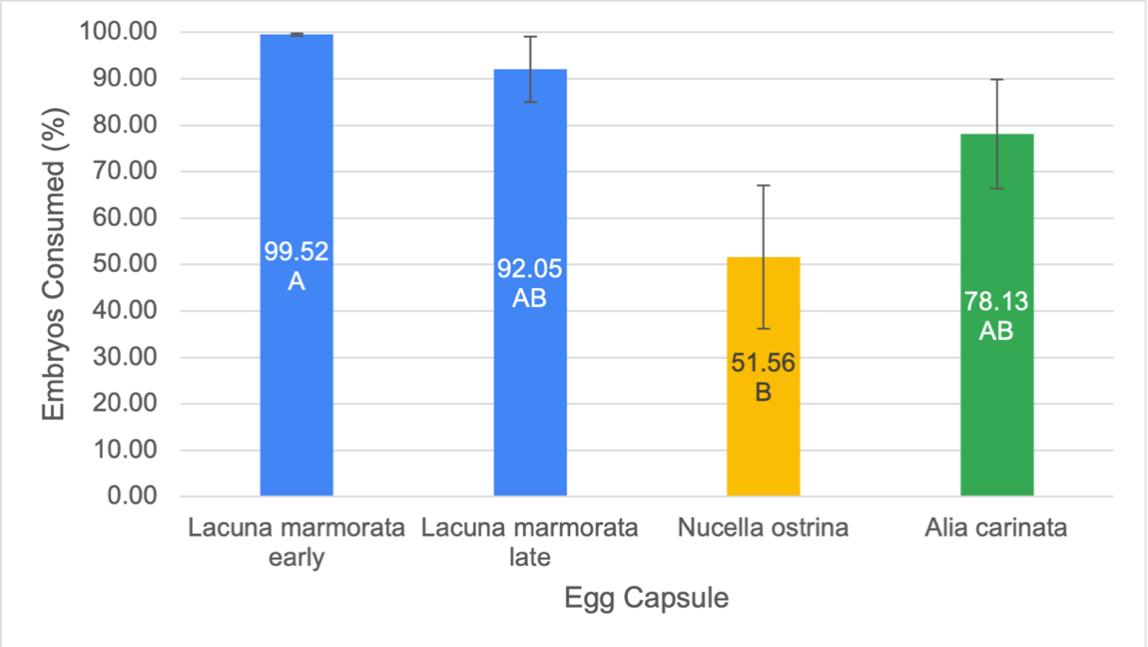

Figure 2: Mean percent of embryo mass that the dove snail consumed for each type of egg capsule that the dove snail preyed on in phase 1. Colors of the bars represent different egg capsules. Different letters labeled on the bars represent significant statistical difference (Tukey HSD, p => 0.0001). Error bars indicate +/- 1 SE.

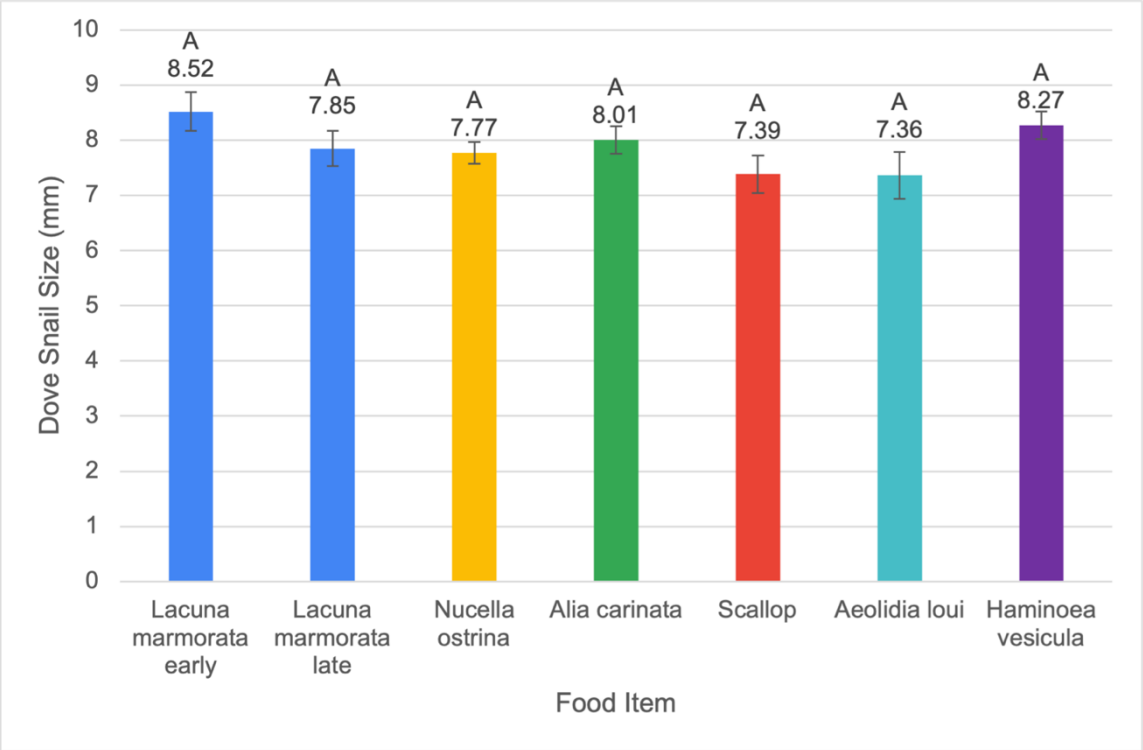

Figure 3: Average dove snail shell size compared across all treatments. Color of the bars represent different food items. Identical letters on bar labels represent no significant statistical difference (Tukey HSD, p > 0.0001). Error bars indicate +/- 1 SE.

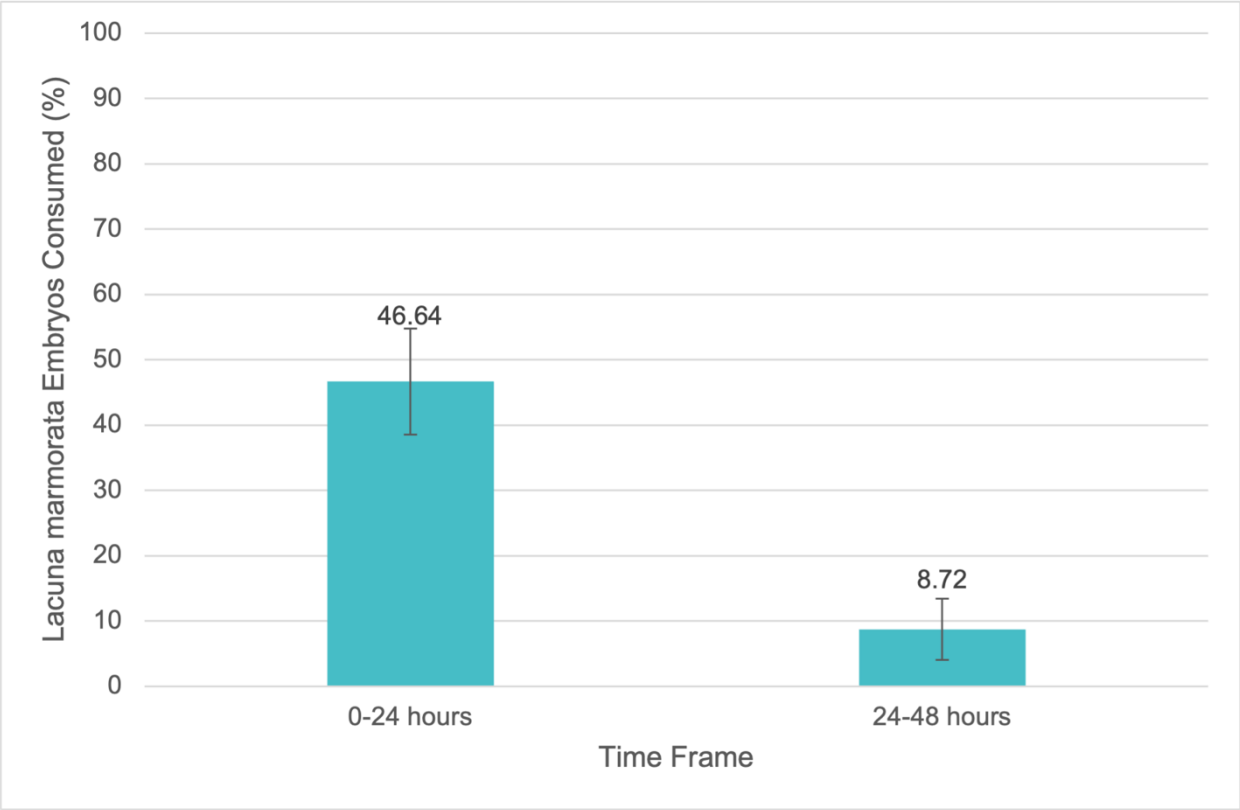

Figure 4: Mean percentage of Lacuna marmorata *embryo mass eaten, divided between the first and second 24 hours of phase 2. Error bars indicate +/- 1 SE.*

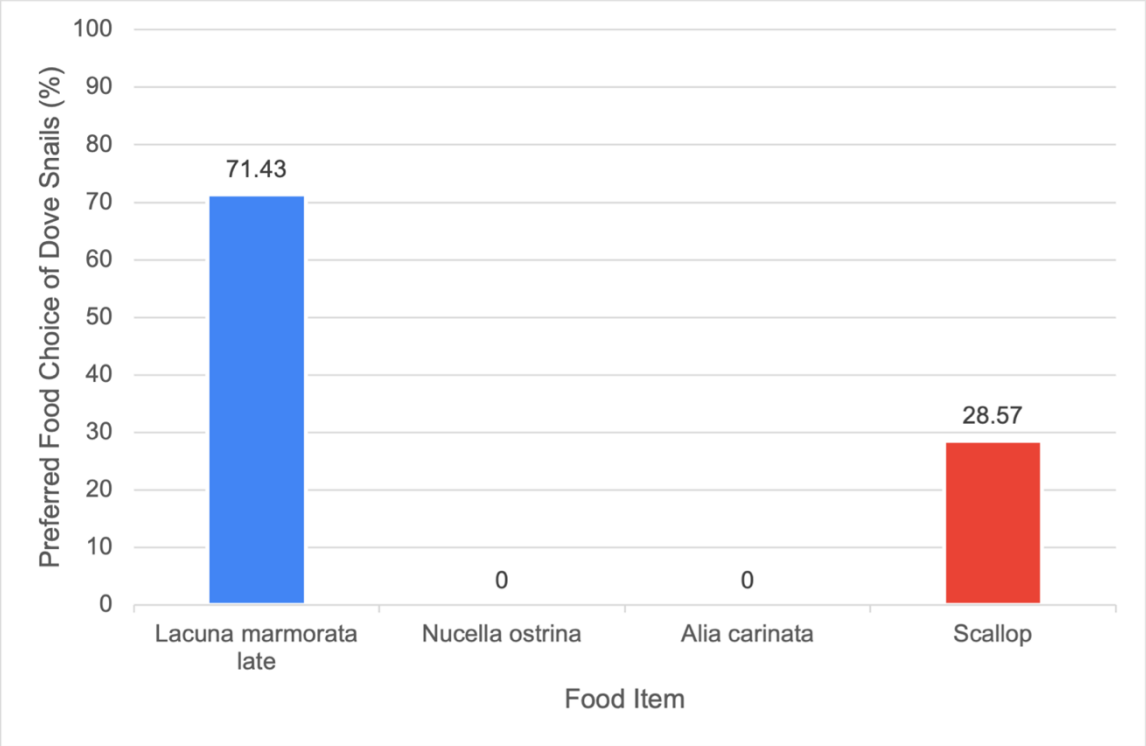

Figure 5: Percentage of dove snails that preferred each food item offered in phase 2 out of 28 dove snails. Colors represent different food items.

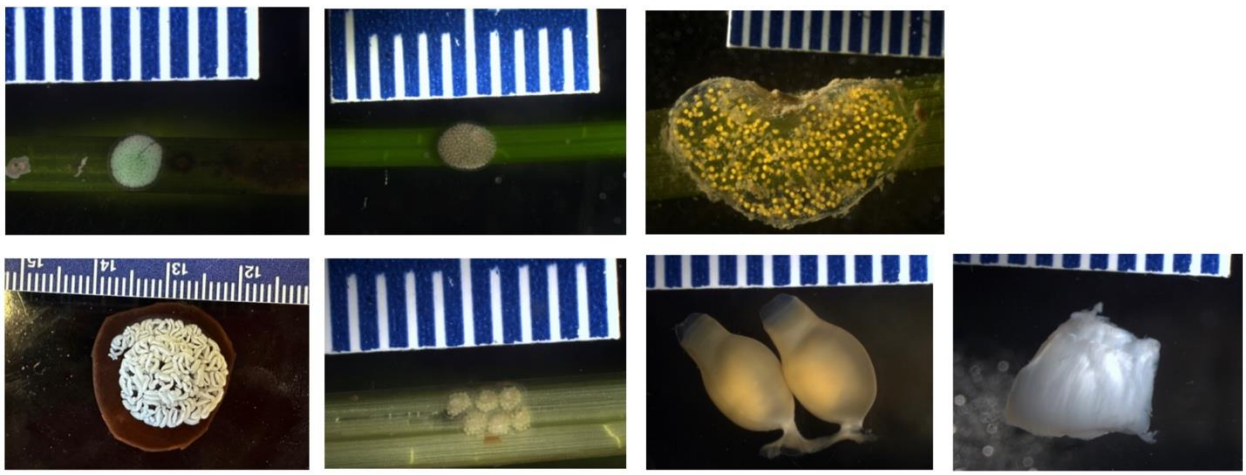

Figure 6: Initial microscope photos of all 7 food items offered in phase 1, trial 1. Top row left to right: Lacuna marmorata *early stage egg capsule,* Lacuna marmorata *late stage egg capsule,* Haminoea vesicula *egg capsule. Bottom row left to right:* Aeolidia loui *egg capsule,* Alia carinata *egg capsules,* Nucella ostrina *egg capsules, raw scallop. Each tick mark on the blue ruler represents 1 millimeter.*

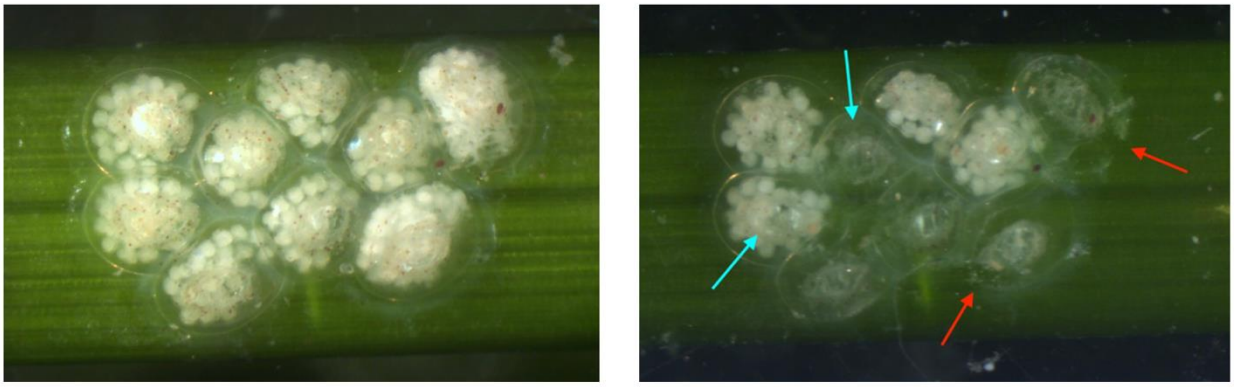

Figure 7: Microscope images of Alia carinata *egg capsules before and after a dove snail fed on the embryos. Blue arrows show the characteristic transparent bubble present on the top of every egg capsule, while the red arrows specifically indicate evidence of dove snail predation.*